

Effects of Stand and Inter-Specific Stocking on Maximizing Standing Tree Carbon Stocks in the Eastern United States

Christopher W. Woodall, Anthony W. D'Amato, John B. Bradford, and Andrew O. Finley

Abstract: There is expanding interest in management strategies that maximize forest carbon (C) storage to mitigate increased atmospheric carbon dioxide. The tremendous tree species diversity and range of stand stocking found across the eastern United States presents a challenge for determining optimal combinations for the maximization of standing tree C storage. Using a nationwide annual forest inventory, we quantified trends in standing tree C across a variety of species mixtures and stocking attributes for 24 of the most common tree species in the eastern United States. We found that as interspecific stocking decreased, such that the majority of stand stocking was in a single species, maximum live tree aboveground carbon (AGC) decreased by 33% in highly stocked stands across all study species. Maximum standing dead tree AGC was not correlated with stand stocking but instead was related to interspecific stocking with AGC storage being reduced by more than 50% as stands became progressively occupied by one tree species. Although the competitive interactions between individual species and/or functional groups (i.e., shade tolerance) can greatly complicate efforts to assess forest C storage opportunities, some basic tenets identified in this study may refine future research hypotheses and broadly identify species mixtures and associated stocking levels that may maximize AGC storage. *FOR. SCI.* 57(5): 365–378.

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GLOBAL MEAN SURFACE TEMPERATURE was higher during the last few decades of the 20th century than during any comparable period during the preceding four centuries (National Research Council 2006) with increasing levels of atmospheric CO₂ and other greenhouse gases identified as major forcing factors (Intergovernmental Panel on Climate Change 2007). Correspondingly, a great need has emerged to mitigate the negative effects of climate change by stabilizing the level of atmospheric CO₂ and thus reducing one of the forcing factors of climate change (Bonan 2008). Forests and their products play a critical role in the carbon (C) cycle by reducing atmospheric levels of CO₂ and other greenhouse gases through emission avoidance and reduction of atmospheric levels (Dixon et al. 1994, Birdsey et al. 2006, Malmshiemer et al. 2008, Ryan et al. 2010). In particular, forests may prevent C emissions through wood substitution (e.g., wood instead of concrete for construction), biomass substitution (e.g., biomass fuels for energy instead of fossil fuels), wildfire behavior modification (e.g., biomass removal before wildfire emissions), and avoided land-use change (e.g., deforestation). In addition, forests can reduce atmospheric concentrations of C through sequestration (e.g., increasing ecosystem C storage through standing live tree growth) and C storage in wood products (e.g., C stored in lumber and furniture) (Ryan et al. 2010).

Given the ability of forests to mitigate C atmospheric concentrations, there is a growing need to evaluate the effects of various forest management practices on C budgets (Birdsey et al. 2006, Lindner et al. 2008, Malmshiemer et al.

2008). Notably, the soils and deadwood components of forest ecosystems serve as important sinks and controls of numerous greenhouse gases (Dixon et al. 1994, Janisch and Harmon 2002, Woodall et al. 2008, Bradford et al. 2009), although these pools are not typically directly managed during normal forest management operations (Harmon 2001). In contrast, aboveground tree biomass is a C sink that can be directly manipulated through forest management (Birdsey et al. 2006, Ryan et al. 2010). The world's forests contains 80% of all aboveground C (Dixon et al. 1994), and, consequently, their management is central to future rates of C sequestration (Bonan 2008).

Recently, forest management strategies for maximizing forest volume or biomass have been applied to the maximization of C sequestration (e.g., even-aged, single-species plantations) (Jacobs et al. 2009). In the past, forest management objectives centered on the efficient production of forest biomass for sawtimber or pulp markets with periodic harvests (Kimmins 1992). In addition to the recent emergence of bioenergy and C markets that suggest the management of forests to maximize C sequestration (Malmshiemer et al. 2008), there is an increasing focus on fostering stand resilience to global change through the maintenance of diverse mixtures of tree species and stand structures in managed forest settings (Evans and Perschel 2009, Puettmann et al. 2009). In the increased application of forest management for the purpose of maximizing aboveground C storage, a novel array of tree species compositions and stand densities will be encountered. Basic tenets of tree species diversity and biomass stocking attributes would greatly aid

Christopher W. Woodall, US Forest Service, Northern Research Station, 1992 Folwell Avenue, St. Paul, MN 55108—Phone: (651) 649-5141; Fax: (651) 649-5140; cwoodall@fs.fed.us. Anthony W. D'Amato, University of Minnesota—damato@umn.edu. John B. Bradford, US Forest Service, Northern Research Station—jbradford@fs.fed.us. Andrew O. Finley, Michigan State University—finleya@msu.edu.

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efforts to estimate the effects that various management activities would have on maximizing aboveground C storage. In the same manner that investigations of mixed species forest productivity have informed approaches to management for traditional forest objectives, such as wood production (e.g., Assmann 1970, Kelty 1992, 2006), it will be important to address questions regarding mixed-species stands and C storage: Can mixed-species stands store more aboveground C than monospecific stands? How do levels of stand stocking and species composition interact to affect the maximization of aboveground C storage?

The goal of this study was to assess how standing tree aboveground C storage relates to stand relative density (RD) and levels of interspecific stocking in the eastern United States. Our specific objectives included (1) determining how mean and 99th percentile aboveground standing tree C stocks (live and dead) vary by levels of stand RD and by the ratio of study species RD to stand RD for the top 24 tree species in the eastern United States (in terms of total volume), (2) determining how differences in tree species functional traits (i.e., shade tolerance) within mixtures affect the results under objective 1, (3) evaluating the slope of the relationship between live tree aboveground carbon (LAGC) and species interspecific stocking, and (4) speculating on opportunities to increase LAGC storage across the entire eastern United States by modifying species composition and density.

Methods

Data

The US Forest Service Forest Inventory and Analysis (FIA) program is the primary source for information about the extent, condition, status, and trends of forest resources in the United States (Smith et al. 2009). FIA applies a nationally consistent sampling protocol using a quasi-systematic design covering all ownerships in the entire nation (national sample intensity is 1 plot/2,428 ha) (Bechtold and Patterson 2005). Land area is stratified using aerial photography or classified satellite imagery to increase the precision of estimates using stratified estimation. Remotely sensed data may also be used to determine whether plot locations have forestland cover; forestland is defined as areas at least 10% stocked with tree species, at least 0.4 ha in size, and at least 36.6 m wide (Bechtold and Patterson 2005). FIA inventory plots established in forested conditions consist of four 7.2-m fixed-radius subplots spaced 36.6 m apart in a triangular arrangement with one subplot in the center (US Forest Service 2007). All trees (standing live and dead) with a dbh of at least 12.7 cm are inventoried on forested subplots. Within each subplot, a 2.07-m microplot offset 3.66 m from the subplot center is established where all live trees with a dbh between 2.5 and 12.7 cm are inventoried. All subplots within the same forest condition (e.g., forest type or stand age) were combined for areal estimates of tree attributes at the hectare level (study plot).

All inventory data are managed in a publicly available FIA database. Data for this study were taken entirely from the FIA database using the most recent annual inventory in 30 eastern states for a total of 72,025 unique observations

(Figure 1). The associated field data are available for download from the FIA DataMart (Forest Inventory and Analysis National Program 2010). Annual inventories for each state were first initiated between 2000 and 2003 and run through 2008, so sample intensities may vary by state.

Analysis

Given the 100+ tree species across the eastern United States, the most common tree species in terms of total live tree aboveground gross cubic foot volume were selected as focus study species (Table 1). All study tree species were assigned to three classes of shade tolerance: tolerant, moderate, and intolerant (Table 1). For the sake of contrast in subsequent analyses, only tolerant and intolerant tree species were evaluated for their C dynamics. For the purpose of computation of stand attributes such as density and species composition attributes, all tree species were considered on each study plot. It should be noted that because of multiple study species occurring on the same study plots, absolute sums of tree species observations are in excess of 72,025 observations.

In this study, stocking was defined as the number of trees per unit area currently in a stand relative to the maximum potential possible (RD). The RD of live trees on every plot is a function of stand density index (SDI) and maximum SDI. SDI was first proposed by Reineke (1933) as a stand density assessment tool based on size-density relationships observed in fully stocked pure or nearly pure stands. A metric version of SDI is defined as the equivalent trees per hectare at a quadratic mean diameter of 25 cm and is formulated as

$$SDI = tph(DBH_q/25)^{1.6}, \quad (1)$$

where tph is number of trees per hectare, and dbh_q is quadratic mean diameter (cm) at breast height (1.4 m) (Long 1985). One way to appropriately determine SDI in stands with non-Gaussian diameter distributions is to determine the SDI for individual dbh classes and then add them for the entire stand (Long and Daniel 1990). This methodology, known both as the additive method and the summation method, has been extensively discussed, from Stage's (1968) initial work to contemporary discourses (Shaw 2000, Ducey and Larson 2003). The SDI summation method is formulated as

$$SDI = \sum tph_i (DBH_i/25)^{1.6}, \quad (2)$$

where dbh_i is the midpoint of the i th diameter class (cm) and tph_i is the number of trees per hectare in the i th diameter class (Shaw 2000).

To determine a RD, the SDI of a stand is typically compared with an empirically observed, species-specific maximum SDI for determining the stand's RD. This process is straightforward in monocultures but confounded in mixed-species stands. To overcome this limitation, Woodall et al. (2005) proposed a methodology to estimate stand-specific maximum SDI regardless of species mixture by using the mean specific gravity of all trees in the stand:

$$E(SDI_{Max}) = 3546.7 - 3927.3(SG_m), \quad (3)$$

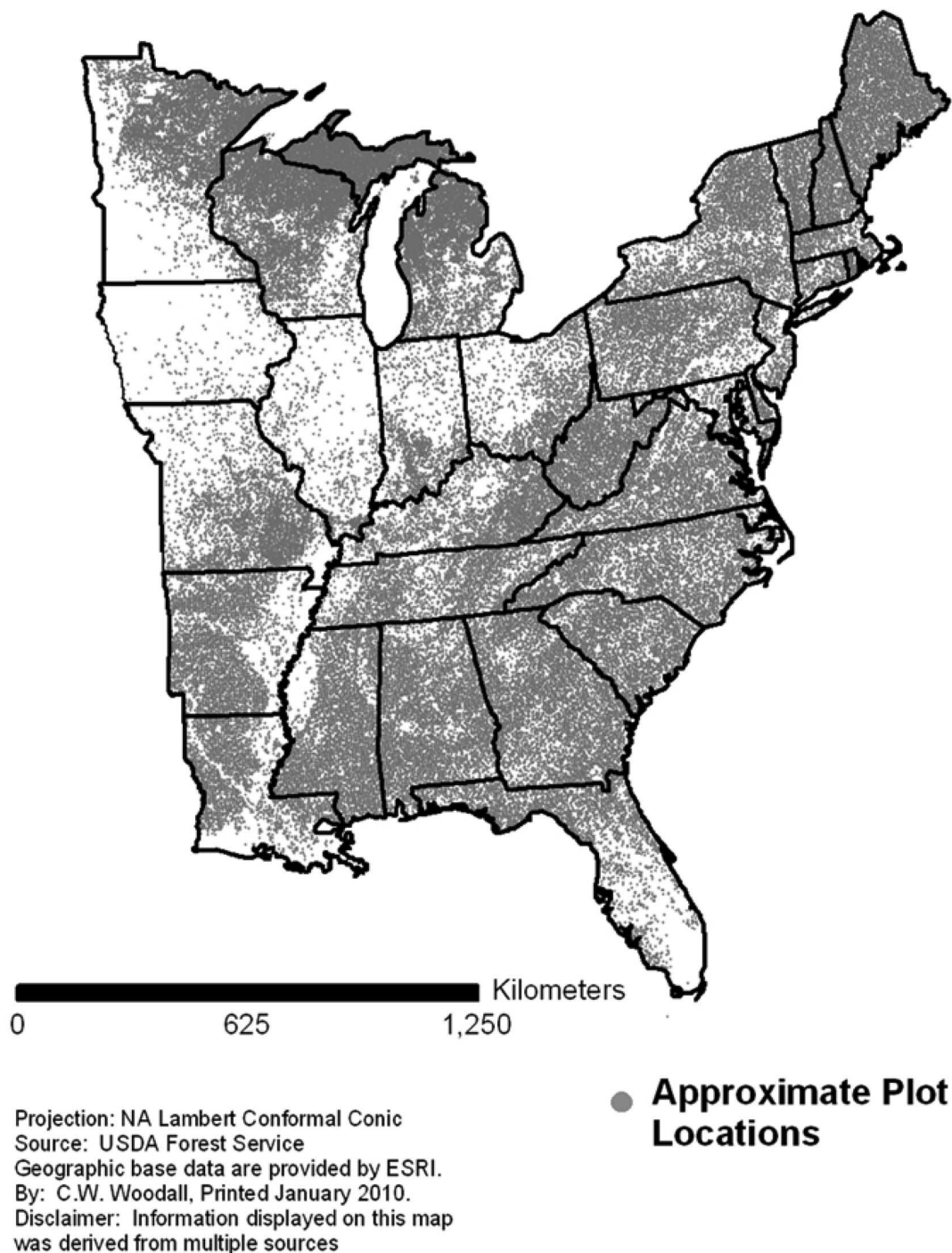


Figure 1. Approximate study plot locations, eastern United States.

where $E(\cdot)$ is statistical expectation and SG_m is the mean specific gravity for all trees in each plot. The higher the specific gravity of a species is, the higher its modulus of elasticity within its bole, the more foliage that can be supported in its crown, and the less trees per unit area needed to support a site-limited amount of leaf area (Dean and Baldwin 1996). Although there is emerging work (Ducey and Knapp 2010a, 2010b) that may improve the coefficients of the Woodall et al. (2005) model at regional scales, the national coefficients proposed by Woodall et al. (2005) should prove adequate for the eastern United States. By using the summation method (Shaw 2000) to determine

the current SDI of a stand and the Woodall et al. (2005) model to predict a maximum SDI (based on the mean specific gravity of all tree species in the plot), the RD of all study plots was determined as current SDI divided by potential maximum SDI.

Interspecific stocking was assessed by comparing the RD of each study species on each plot to the RD of the plot (species composition purity ratio [SCP]). For example, if a plot is 100% stocked with white oak (*Quercus alba* L.) then its stand RD and white oak SCP ratio would be 1.0. In contrast, if it is 100% stocked, but only 10% of the stand is stocked with white oak and 90% of the other stocking is

Table 1. Common and scientific name of study tree species along with number of observations and shade tolerance class.

Common name	Genus and species	No. observations	Tolerance class
Balsam fir	<i>Abies balsamea</i>	10,432	Tolerant
Shortleaf pine	<i>Pinus echinata</i>	4,974	Intolerant
Slash pine	<i>Pinus elliottii</i>	3,619	Intolerant
Eastern white pine	<i>Pinus strobus</i>	7,570	Moderate
Loblolly pine	<i>Pinus taeda</i>	16,335	Intolerant
Eastern hemlock	<i>Tsuga canadensis</i>	5,634	Tolerant
Red maple	<i>Acer rubra</i>	37,138	Tolerant
Sugar maple	<i>Acer saccharum</i>	16,502	Tolerant
Yellow birch	<i>Betula alleghaniensis</i>	6,522	Moderate
Pignut hickory	<i>Carya glabra</i>	7,876	Intolerant
American beech	<i>Fagus grandifolia</i>	9,324	Tolerant
White ash	<i>Fraxinus americana</i>	10,547	Moderate
Sweetgum	<i>Liquidambar styraciflua</i>	16,639	Intolerant
Yellow-poplar	<i>Liriodendron tulipifera</i>	11,885	Intolerant
Quaking aspen	<i>Populus tremuloides</i>	10,249	Intolerant
Black cherry	<i>Prunus serotina</i>	16,525	Intolerant
White oak	<i>Quercus alba</i>	17,537	Moderate
Scarlet oak	<i>Quercus coccinea</i>	4,844	Moderate
Southern red oak	<i>Quercus falcata</i>	6,152	Moderate
Water oak	<i>Quercus nigra</i>	9,175	Moderate
Chestnut oak	<i>Quercus prinus</i>	5,320	Moderate
Northern red oak	<i>Quercus rubra</i>	13,759	Moderate
Post oak	<i>Quercus stellata</i>	6,312	Moderate
Black oak	<i>Quercus velutina</i>	9,771	Moderate

occupied by other species, then its plot RD would be 1.0 and its white oak SCP ratio would be 0.1. The SCP ratio approximates a continuum of interspecific stocking from mixed to “more pure” and in conjunction with the stand RD provides an overall measure of the overall stand stocking level and the contribution of the focal species to that stocking.

The LAGC and dead tree aboveground carbon (DAGC) stocks were determined following procedures documented in Heath et al. (2009), in which regional volume equations (Woodall et al. 2011) were used to determine sound cubic foot volume, which is then converted to biomass (reduced by 50% for C) using species’ specific gravity values (Miles and Smith 2009) and assigning C to tree components using the component ratio method. The mean and 99th percentile LAGC and DAGC stocks were calculated for a matrix of stand stocking and SCP ratios: three classes of stand stocking (understocked, 0.0–0.3 RD; well-stocked, 0.3–0.6 RD; and overstocked, >0.6 RD) and 10 classes of SCP ratios (0.1 intervals). The 99th percentile was selected as a surrogate for maximum (100th percentile) LAGC stocks to avoid the inclusion of outliers potentially resulting from measurement error. Significant differences between means were tested using an analysis of variance model (differences significant at $P < 0.05$). In addition, the 99th percentile of LAGC stocks was calculated for the three classes of stand stocking and four classes of shade tolerance competition (tolerant study species with tolerant competition, tolerant study species with intolerant competition, and vice versa). The shade tolerance of competition for each study tree species on each plot was assigned to either tolerant or intolerant classes if the majority (>50%) of competing RD was in the respective shade tolerance classes.

Quantile regression was used to relate the 95th percentile of the LAGC response variable to the SCP ratio, $LAGC = b_0 + b_1SCP$ ratio, for the classes of stand stocking and three classes

of study species shade tolerance (tolerant, moderate, and intolerant). Regression coefficients were estimated using the SAS quantreg procedure (for example, see Zhang et al. 2005). The 95th percentile was selected because it was the highest percentile achieved that had a majority of estimated coefficients with a 0.05 probability of a larger value of the test statistic.

Finally, to evaluate the opportunities to increase LAGC storage in eastern US forests, all inventory plots with no species restrictions were extracted using the most recent inventory cycles. With 92,225 individual observations, the relationship between 95th percentile LAGC as a function of RD was fit using quantile regression for major forest type groups. It should be acknowledged that irrespective of stand RD, site quality should affect maximum LAGC. Future efforts to estimate C maximization beyond this study’s initial exploration should consider site quality as an additional independent variable. This study’s model ($LAGC = b_0 + b_1RD$) estimates the 95th percentile of LAGC achieved within forest type groups at each level of RD. For the sake of comparison, ordinary least-squares regression was used to fit the same data and model approximating mean LAGC. An interpolated map of the difference between a plot’s current LAGC and estimated 95th percentile LAGC was created using inverse distance weighting (Johnston et al. 2001) in ARCGIS with a 1 km \times 1 km nonforest mask applied. In essence, this methodology provides an approximation of the difference between current LAGC storage and the maximum potential LAGC by forest type group and level of stand RD across forests of the eastern United States.

Results

Estimates of mean stand-level LAGC changed significantly across levels of stand RD for all species ($P = 0.0018$)

(Figure 2A) and for most individual species (Table 2). Mean LAGC across all SCP ratios ranged from 6.52 (balsam fir) to 23.49 Mg/ha (northern red oak), from 21.70 (balsam fir) to 81.63 Mg/ha (yellow-poplar), and from 37.10 (balsam fir) to 127.20 Mg/ha (yellow-poplar) for understocked, well-stocked, and overstocked stands, respectively (Table 2). For some species, the highest mean LAGC was achieved

in the purest stands (e.g., yellow-poplar; Table 2); however, for most species the highest mean LAGC (within a given stocking level) was achieved in mixed-species compositions (e.g., loblolly pine; Table 2). Mean LAGC across all species ranged between 15 and 20, 45 and 50, and 75 and 85 Mg/ha, for understocked, well-stocked, and overstocked stands, respectively (Figure 2A). Within the three classes of stand

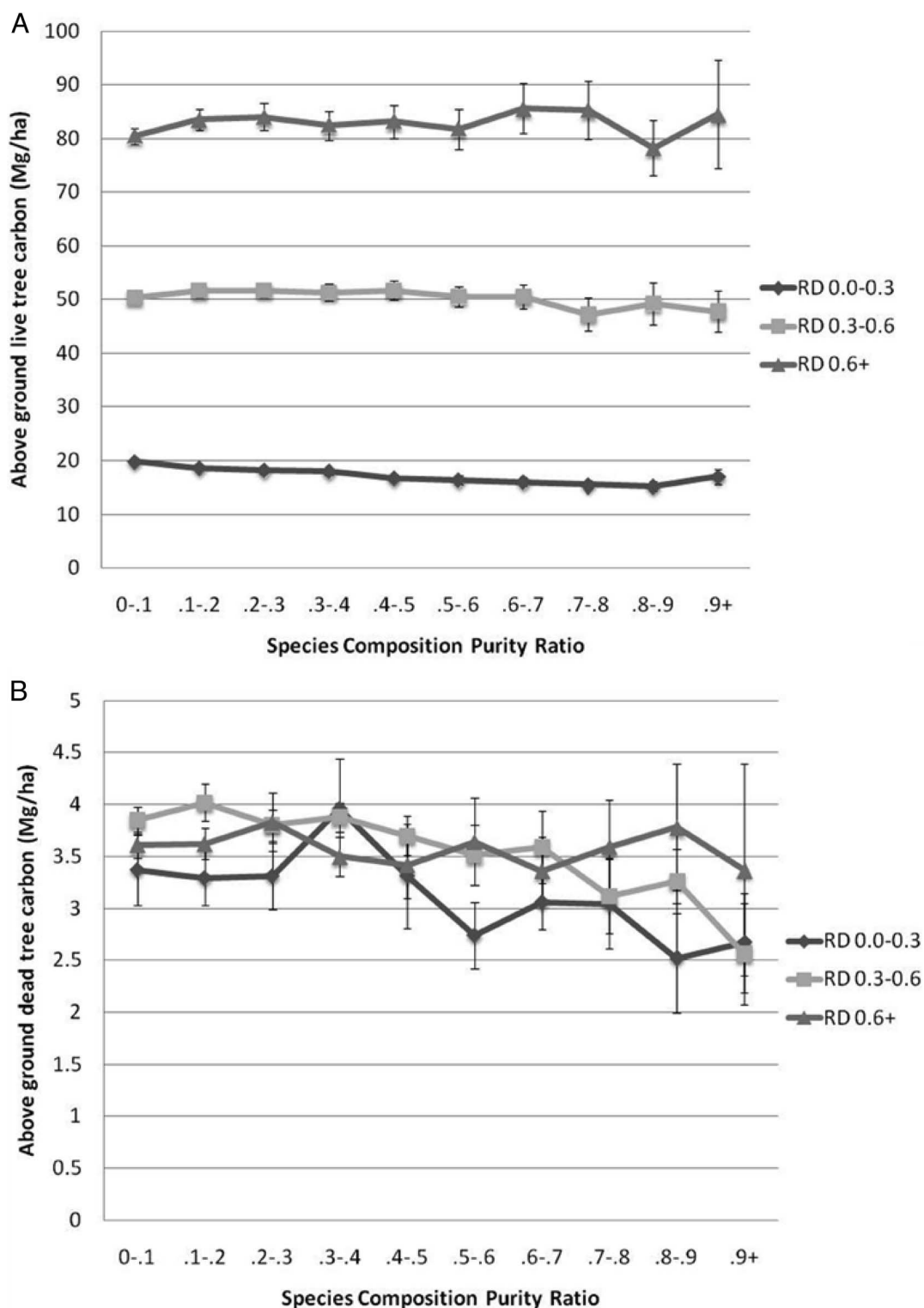


Figure 2. Means and associated SEs of aboveground live tree carbon for all study species for (A) standing live and (B) standing dead trees by three levels of stand stocking (understocked, well-stocked, and overstocked) and 10 levels of increasing species composition purity (stocking assessment based on RD).

Table 2. Mean aboveground live tree carbon for each study species by three levels of stand stocking (understocked, well-stocked, and overstocked) and three levels of increasing species composition purity (stocking assessment based on RD).

Study species	Understocked (RD < 0.3)			Well-stocked (RD 0.3–0.6)			Overstocked (RD > 0.6)		
	SCP 1	SCP 2	SCP 3	SCP 1	SCP 2	SCP 3	SCP 1	SCP 2	SCP 3
	(Mg/ha)								
Balsam fir	<i>14.48^a</i>	<i>10.24</i>	<i>6.52</i>	<i>40.51</i>	<i>29.68</i>	<i>21.70</i>	<i>65.55</i>	<i>47.55</i>	<i>37.10</i>
Shortleaf pine	<i>18.15</i>	<i>15.63</i>	<i>15.63</i>	<i>47.36</i>	<i>47.92</i>	<i>39.78</i>	<i>73.30</i>	<i>68.01</i>	<i>68.39</i>
Slash pine	<i>15.15</i>	<i>14.45</i>	<i>14.41</i>	<i>41.35</i>	<i>41.52</i>	<i>37.23</i>	<i>75.55</i>	<i>74.64</i>	<i>64.17</i>
Eastern hite pine	<i>17.91</i>	<i>16.87</i>	<i>18.10</i>	<i>49.31</i>	<i>55.95</i>	<i>58.21</i>	<i>80.34</i>	<i>90.67</i>	<i>94.28</i>
Loblolly pine	<i>15.42</i>	<i>13.98</i>	<i>14.55</i>	<i>45.79</i>	<i>43.28</i>	<i>36.00</i>	<i>76.36</i>	<i>69.13</i>	<i>57.73</i>
Eastern hemlock	<i>22.06</i>	<i>19.86</i>	<i>20.38</i>	<i>56.10</i>	<i>54.65</i>	<i>58.90</i>	<i>89.03</i>	<i>91.77</i>	<i>87.82</i>
Red maple	<i>18.80</i>	<i>15.41</i>	<i>14.29</i>	<i>51.82</i>	<i>50.23</i>	<i>48.82</i>	<i>84.58</i>	<i>81.92</i>	<i>84.31</i>
Sugar maple	<i>21.40</i>	<i>20.75</i>	<i>21.44</i>	<i>55.09</i>	<i>57.65</i>	<i>58.41</i>	<i>89.32</i>	<i>87.84</i>	<i>90.01</i>
Yellow birch	<i>19.44</i>	<i>14.78</i>	<i>11.45</i>	<i>50.97</i>	<i>53.25</i>	<i>56.65</i>	<i>80.12</i>	<i>77.63</i>	<i>92.93</i>
Pignut hickory	<i>22.17</i>	<i>18.49</i>	<i>13.02</i>	<i>57.99</i>	<i>57.64</i>	<i>33.88</i>	<i>89.54</i>	<i>86.04</i>	<i>90.48</i>
American beech	<i>23.09</i>	<i>19.49</i>	<i>17.13</i>	<i>59.85</i>	<i>58.11</i>	<i>49.53</i>	<i>93.46</i>	<i>88.24</i>	<i>77.74</i>
White ash	<i>20.09</i>	<i>16.64</i>	<i>15.96</i>	<i>55.09</i>	<i>53.92</i>	<i>43.03</i>	<i>87.83</i>	<i>95.25</i>	<i>98.95</i>
Sweetgum	<i>17.55</i>	<i>13.08</i>	<i>9.86</i>	<i>48.30</i>	<i>46.87</i>	<i>44.55</i>	<i>78.71</i>	<i>79.43</i>	<i>79.41</i>
Yellow-poplar	<i>19.73</i>	<i>19.94</i>	<i>20.38</i>	<i>56.14</i>	<i>65.82</i>	<i>81.63</i>	<i>89.60</i>	<i>111.28</i>	<i>127.20</i>
Quaking aspen	<i>15.39</i>	<i>12.33</i>	<i>10.61</i>	<i>41.58</i>	<i>33.72</i>	<i>27.83</i>	<i>66.57</i>	<i>56.17</i>	<i>50.59</i>
Black cherry	<i>18.33</i>	<i>13.12</i>	<i>10.51</i>	<i>48.60</i>	<i>51.58</i>	<i>56.53</i>	<i>79.61</i>	<i>107.04</i>	<i>102.86</i>
White oak	<i>20.16</i>	<i>20.20</i>	<i>18.64</i>	<i>53.22</i>	<i>55.69</i>	<i>55.36</i>	<i>84.83</i>	<i>85.64</i>	<i>84.20</i>
Scarlet oak	<i>21.17</i>	<i>20.18</i>	<i>17.13</i>	<i>54.53</i>	<i>55.38</i>	<i>41.32</i>	<i>84.97</i>	<i>86.76</i>	<i>66.63</i>
Southern red oak	<i>18.25</i>	<i>17.85</i>	<i>17.70</i>	<i>48.28</i>	<i>54.12</i>	<i>58.13</i>	<i>74.91</i>	<i>93.64</i>	—
Water oak	<i>16.77</i>	<i>14.34</i>	<i>14.21</i>	<i>45.36</i>	<i>46.41</i>	<i>45.32</i>	<i>73.63</i>	<i>79.37</i>	<i>97.66</i>
Chestnut oak	<i>23.46</i>	<i>23.08</i>	<i>21.37</i>	<i>60.99</i>	<i>61.11</i>	<i>61.78</i>	<i>95.15</i>	<i>92.01</i>	<i>92.75</i>
Northern red oak	<i>21.37</i>	<i>20.61</i>	<i>23.49</i>	<i>55.38</i>	<i>60.37</i>	<i>63.82</i>	<i>88.69</i>	<i>101.78</i>	<i>105.82</i>
Post oak	<i>17.60</i>	<i>14.55</i>	<i>11.48</i>	<i>46.02</i>	<i>39.71</i>	<i>36.62</i>	<i>70.55</i>	<i>56.34</i>	<i>52.45</i>
Black oak	<i>20.05</i>	<i>18.70</i>	<i>18.60</i>	<i>53.47</i>	<i>51.23</i>	<i>47.86</i>	<i>84.49</i>	<i>82.14</i>	<i>79.24</i>

SCP: 1 = 0.0–0.33; 2 = 0.34–0.66; and 3 = 0.67–1.00.

^a Italics indicate $P < 0.05$.

stocking, there were no consistent trends in LAGC between SCP ratios. Estimates of mean DAGC for all study species had no obvious trends by either stand density or SCP ratios (Figure 2B).

The 99th percentile of LAGC varied across classes of stand stocking and SCP ratios (Table 3). Across all classes of SCP ratios, the 99th percentile of LAGC ranged from 19.46 (balsam fir) to 70.37 Mg/ha (yellow-poplar), from 48.13 (balsam fir) to 174.81 Mg/ha (yellow-poplar), and from 67.72 (balsam fir) to 223.83 Mg/ha (water oak) for understocked, well-stocked, and overstocked stands, respectively (Table 3). For individual species, there were some apparent trends in the 99th percentiles of LAGC across classes of SCP ratios. For example, some species (e.g., balsam fir, pignut hickory, quaking aspen, and post oak) had fairly substantial decreases in 99th percentile LAGC as SCP ratios increased across all classes of stand stocking; however, similar trends were not seen within other species (e.g., red maple, white ash, and water oak). Across all study species, means of the 99th percentile LAGC ranged between 40 and 50, 70 and 105, and 110 and 165 Mg/ha, for understocked, well-stocked, and overstocked stands, respectively (Figure 3A). Overall, as stand stocking increased, the average 99th percentile of LAGC for all study species decreased with increasing stand purity (increasing SCP ratios) along with a difference in the average 99th percentile LAGC between classes of stand stocking. In contrast, as stand stocking increased, the 99th percentile of DAGC decreased with increasing stand purity (increasing SCP ra-

tios); however, there was no difference in the average 99th percentile DAGC between classes of stand stocking (Figure 3B). The mean 99th percentile of DAGC across all study species ranged between 20 to 27 Mg/ha when the SCP ratio was 0.3 compared with a range of 7 to 14 Mg/ha when the SCP ratio was greater than 0.7.

The effects of tree species shade tolerance attributes and stand stocking on 99th percentile LAGC were examined across classes of stand stocking and SCP ratios (Figure 4A–C). The shade tolerance of study species appeared to have no effect on differences in 99th percentiles of LAGC, whereas tolerance of competing tree species composition appeared to have an effect on LAGC in well-stocked stands. If the majority of competing RD was composed of shade-tolerant species, there were minimal decreases in LAGC (Figure 4C). In contrast, if the majority of competing RD were shade-intolerant species, there appeared to be more substantial reductions in 99th percentiles of LAGC as SCP ratios increased.

To further evaluate the maximization of LAGC across a myriad of stocking and species mixtures, a model of 95th percentile LAGC dependent on SCP ratios was fit using quantile linear regression by classes of stand stocking and study species shade tolerance (Table 4). Estimates of the y -intercept coefficient did not appear to vary across classes of shade tolerance but did vary across classes of stand stocking. Estimates of the SCP ratio coefficient are an indicator of how the maximization of LAGC storage is affected by increasing stand species purity. The SCP ratio

Table 3. 99th percentile of aboveground live tree carbon for each study species by three levels of stand stocking (understocked, well-stocked, and overstocked) and three levels of increasing species composition purity (stocking assessment based on RD).

Study species	Understocked (RD < 0.3)			Well-stocked (RD 0.3–0.6)			Overstocked (RD > 0.6)		
	SCP 1	SCP 2	SCP 3	SCP 1	SCP 2	SCP 3	SCP 1	SCP 2	SCP 3
(Mg/ha).....								
Balsam fir	36.89	30.20	19.46	81.26	59.92	48.13	126.48	82.45	67.72
Shortleaf Pine	50.75	44.74	38.04	103.19	93.30	105.20	145.71	147.55	129.75
Slash pine	48.04	48.82	48.60	94.60	95.38	95.05	178.06	162.01	136.99
Eastern white pine	47.25	46.31	54.85	101.46	112.13	114.01	155.33	195.39	147.91
Loblolly pine	49.77	49.16	50.80	106.80	105.89	94.49	159.59	157.55	139.59
Eastern hemlock	51.04	47.91	55.17	110.02	93.90	96.73	181.31	156.52	130.44
Red maple	51.00	45.30	45.39	109.71	101.41	108.43	175.32	152.55	171.67
Sugar maple	52.43	53.17	54.18	110.72	109.93	104.64	174.16	155.33	147.12
Yellow birch	49.86	38.29	38.22	97.60	97.47	74.87	149.79	139.57	131.34
Pignut hickory	53.46	47.57	45.73	114.60	110.56	48.98	167.14	140.85	111.08
American beech	56.45	51.87	57.45	116.81	106.59	110.02	178.91	162.48	126.84
White ash	51.07	51.22	64.02	110.72	115.96	122.49	170.55	190.45	133.13
Sweetgum	51.67	45.64	47.25	110.69	112.73	103.61	172.36	163.37	161.94
Yellow-poplar	53.46	58.10	70.37	114.39	134.01	174.81	182.05	214.01	198.19
Quaking aspen	39.81	33.83	33.83	83.82	69.45	66.09	126.36	101.08	95.70
Black cherry	52.01	47.68	38.42	106.12	109.98	142.10	163.35	200.00	150.93
White oak	50.71	52.88	50.06	107.89	110.96	99.49	169.90	164.25	165.75
Scarlet oak	49.09	48.73	51.67	108.03	99.98	55.53	159.43	187.79	104.87
Southern red oak	53.22	56.22	60.28	111.37	119.71	90.27	158.53	194.09	170.37
Water oak	49.74	47.03	55.06	104.64	109.19	131.97	164.83	223.83	205.61
Chestnut oak	51.54	51.74	51.00	115.27	113.41	111.05	175.59	165.41	199.24
Northern red oak	54.65	54.25	61.76	110.98	111.08	113.36	169.99	194.38	160.99
Post oak	47.21	43.44	42.82	97.96	83.48	59.20	154.88	104.06	83.95
Black oak	50.01	49.16	71.02	111.05	102.85	96.08	163.11	166.56	95.79

SCP: 1 = 0.0–0.33; 2 = 0.34–0.66; and 3 = 0.67–1.00.

coefficient was negative across all classes of stand stocking regardless of species' shade tolerance. When shade tolerance was taken into account, intolerant and tolerant tree species SCP ratio coefficients were even more negative, whereas study tree species with moderate shade tolerance had positive slopes across all classes of stand stocking. The majority of moderate shade tolerance species in this study were oak species. Given the tens of thousands of observations in this study, nonintuitive combinations of species' tolerances and RDs cannot be elucidated on an individual stand basis. However, occurrences of stands well-stocked with shade-tolerant species with minimal competition from moderate to intolerant species occurred in disturbed areas where residual intolerant species occupied the overstory and shade-tolerant saplings were well-stocked in the understory (e.g., coastal Louisiana with remnant green ash [*Fraxinus pennsylvanica*], black willow [*Salix nigra*], and water tupelo [*Nyssa aquatica*] in the overstory with red maple saplings in the understory).

Finally, to speculate on opportunities to increase LAGC storage through stand management activities (e.g., species selection, stand structure alteration, and site improvement), the difference between current LAGC and potential maximum storage was estimated by forest type group (for definition, see Woudenberg et al. 2010) and levels of stand stocking. Effectively, the difference between current mean LAGC and 95th percentile LAGC was determined (Figure 5). It should be strongly noted that in this study we did not explicitly conduct management treatments on forest stands; rather management effects were inferred through current

stand conditions across the eastern United States. If current forest type groups were managed using systems that favored LAGC maximization, perhaps a $\geq 50\%$ increase in storage could occur (assuming that stand RD remains static) (Table 5). Opportunities to increase LAGC storage appear randomly dispersed across forests of the United States with some focal areas in central hardwoods, the upper peninsula of Michigan, areas of upper New England, and pine forests of the southeast (Figure 6). However improbable, if stand management were oriented toward maximizing LAGC and stand stocking were maximized (RD = 1), then LAGC storage could be increased 3–4 times current stocks (Table 5). The veracity of these results should be further explored in actual management treatments applied in research plots across the variety of stand conditions found in the eastern United States.

Discussion

One of the many foci of forest management for the past 100 years has been the maximization of a stand's pulpwood or sawtimber volume over a given rotation length, typically at a culmination of mean annual increment (Newman 1988). Numerous management guidelines (for examples, see Gingrich 1967, Drew and Flewelling 1979) and compendiums of growth and yield information (for example, see Assmann 1970) have been used to maximize the production of these forest products. The results of this study in the context of emerging C and biomass economies present new complexities related to forest management. Not only can increasing tree species diversity

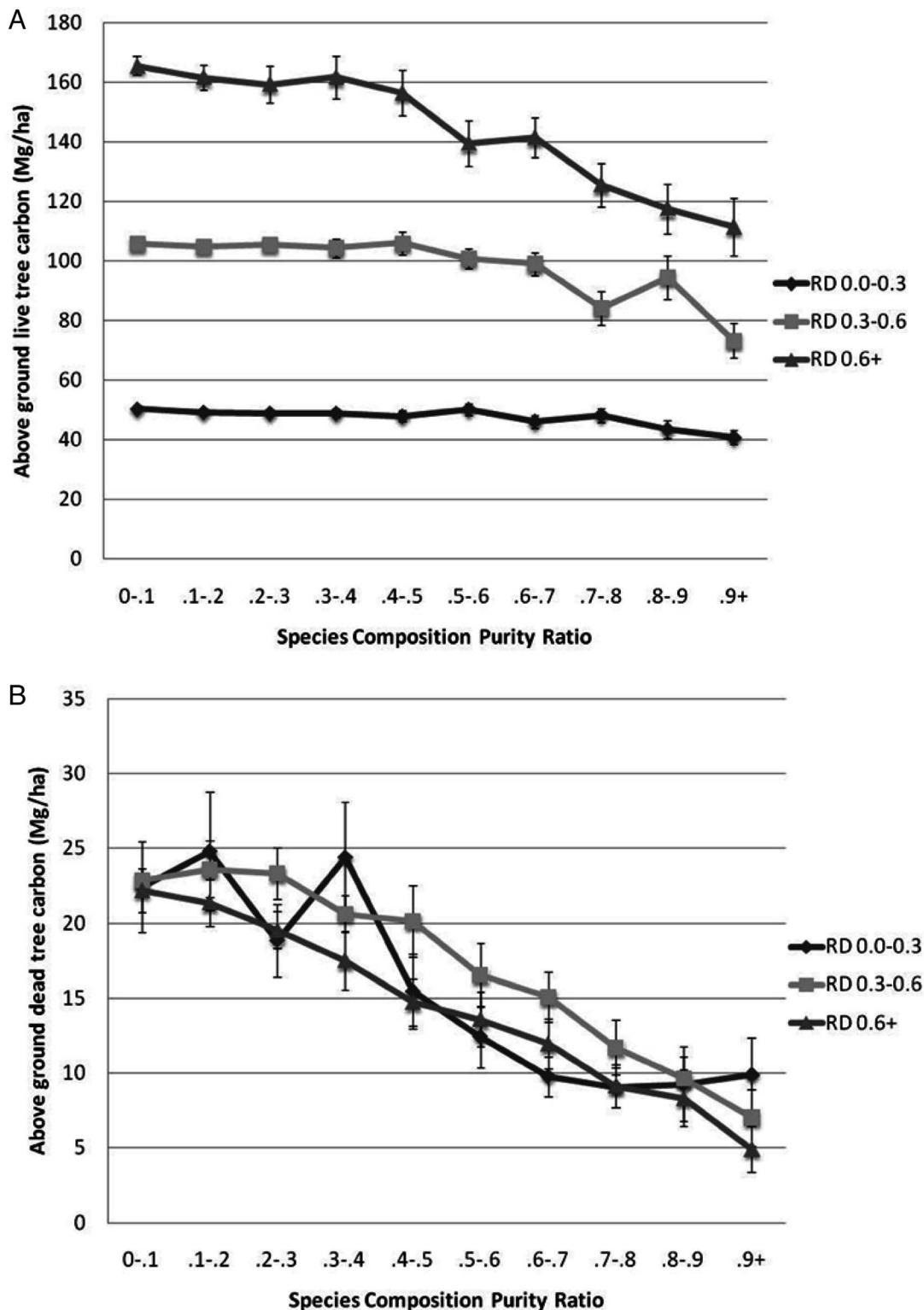


Figure 3. Means and associated SEs of the 99th percentile aboveground live tree carbon for all study species for (A) standing live and (B) standing dead trees by three levels of stand stocking (understocked, well-stocked, and overstocked) and 10 levels of increasing species composition purity (stocking assessment based on RD).

and functional groups increase a forest's resilience to changing climate and disturbance regimes (Caspersen and Pacala 2001, Diaz and Cabido 2001, Puettmann et al. 2009, Paquette and Messier 2010), but it may also provide opportunities to increase the maximum potential LAGC. This study extensively examined current stand attributes across the eastern United

States, thus inferring the management implications of observed trends and stand/site interactions of individual inventory plots. It is strongly suggested that the findings of this study be further evaluated through intensive research plots. Caveats aside, the results of this study may provide some basic tenets of forest stocking among diverse arrays of species composition to aid

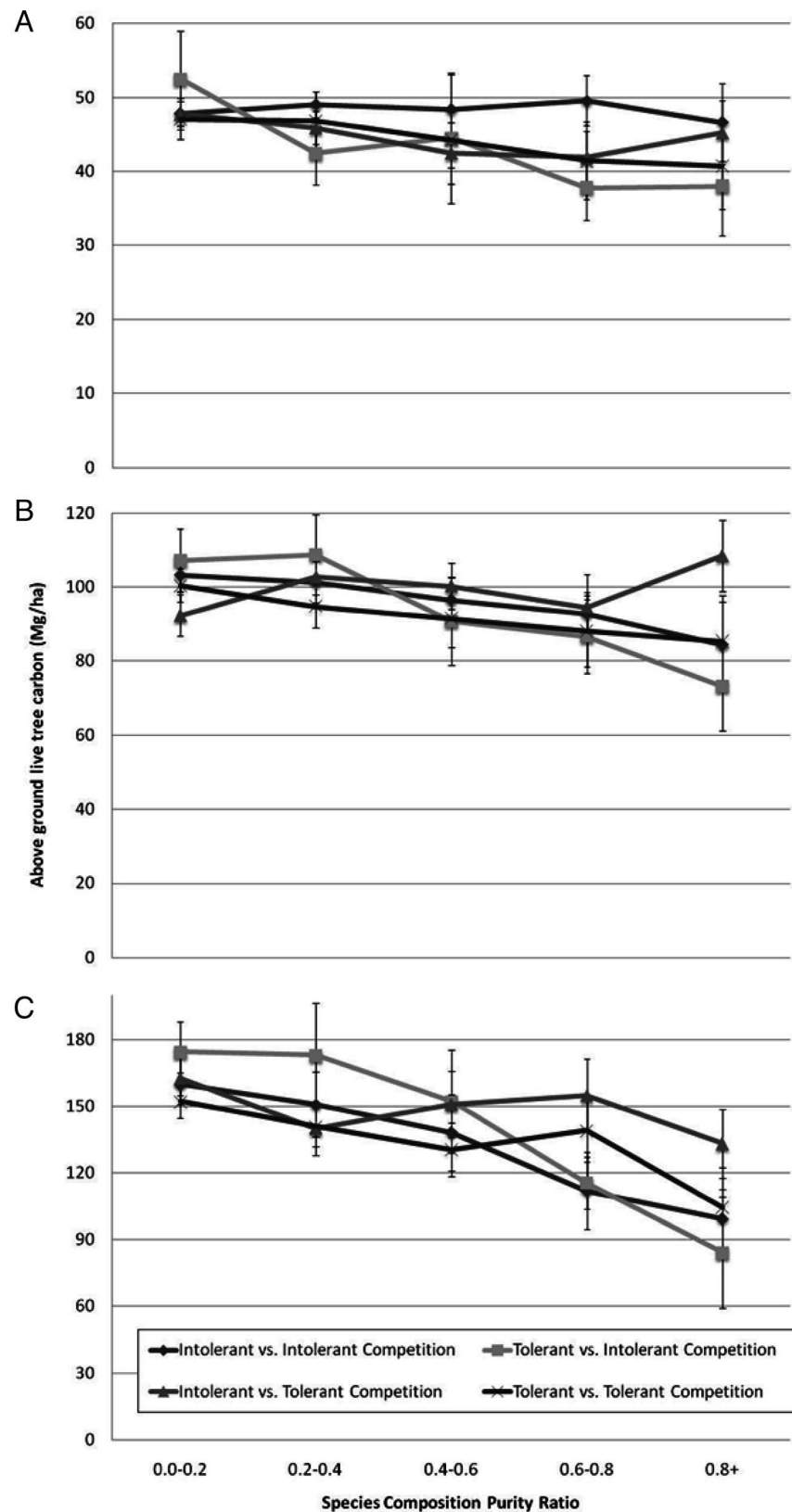


Figure 4. Means and associated SEs of the 99th percentile of aboveground live tree carbon for all study species by four scenarios of shade tolerance competitive interactions (intolerant study species versus competition from intolerant species, tolerant study species versus competition from intolerant species, intolerant study species versus competition from tolerant species, and tolerant study species versus competition from tolerant species; at least 50% of competing RD comes from the shade tolerance class of interest) by five levels of increasing species composition purity (stocking assessment based on RD) for three levels of stand stocking: (A) understocked; (B) well-stocked; and (C) overstocked.

Table 4. 95th percentile regression results for aboveground live tree carbon = RD ratio by classes of shade tolerance and level of stand stocking (stocking based on RD).

Stand stocking	Species category	b_0 intercept (Mg/ha)			b_1 SCP ratio		
		Estimate	SE	P value	Estimate	SE	P value
Understocked (RD < 0.3)	All	40.24	0.19	<0.0001	-4.70	0.59	<0.0001
	Intolerant	39.88	0.36	<0.0001	-6.20	0.92	<0.0001
	Moderate	39.75	0.29	<0.0001	1.48	1.12	0.1852
	Tolerant	40.57	0.31	<0.0001	-7.56	0.77	<0.0001
Well-stocked (RD 0.3–0.6)	All	89.80	0.18	<0.0001	-3.02	0.83	0.0003
	Intolerant	89.91	0.44	<0.0001	-7.37	2.11	0.0005
	Moderate	88.38	0.39	<0.0001	6.39	1.86	0.0006
	Tolerant	91.12	0.44	<0.0001	-8.75	1.71	<0.0001
Overstocked (RD > 0.6)	All	137.03	0.46	<0.0001	-3.80	2.32	0.1013
	Intolerant	138.49	0.91	<0.0001	-14.05	4.86	0.0039
	Moderate	133.77	0.89	<0.0001	17.31	4.95	0.0005
	Tolerant	139.47	0.79	<0.0001	-15.78	2.84	<0.0001

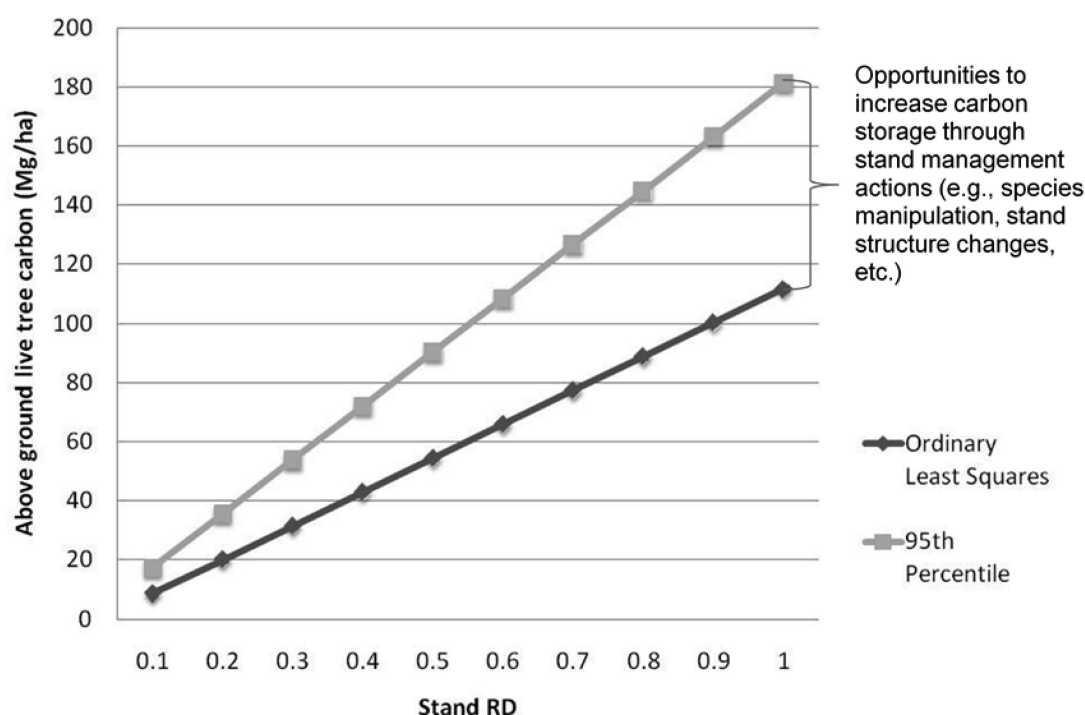


Figure 5. Ordinary least-squares regression and 95th percentile quantile regression estimates for LAGC across increasing levels of stand RD, eastern United States.

foresters with maximizing LAGC and to refine future research hypotheses.

Although these results indicate a clear positive relationship between stand stocking and mean LAGC across the eastern United States, the effects of interspecific stocking for LAGC are unclear. Despite numerous studies documenting the positive influence of species diversity on ecosystem functions (e.g., biomass accretion) (Naeem et al. 1994, Tilman et al. 1997, 2001, Chapin et al. 2000, Schwartz et al. 2000), our results suggest that mean LAGC stocks do not appear to vary across levels of tree diversity, a result identified in other work examining aboveground carbon stocks at localized scales (Kirby and Potvin 2007). Thus, examining the mean attributes of a myriad of species compositions and their respective RD does not appear to be useful for informing management regimes for maximizing LAGC and

DAGC stocks. In contrast, the influence of tree interspecific RD on LAGC was quite pronounced when the 99th percentile of LAGC was examined. In particular, the trends with the 99th percentile of LAGC indicate that, for many tree species assemblages, increasing tree species diversity might increase maximum LAGC storage. This relationship between maximum LAGC and species has important implications for emerging objectives such as identifying optimal species mixtures for forest management strategies aimed to provide carbon and biodiversity benefits (Hartley 2002, Paquette and Messier 2010). Previous work examining productivity within mixed-species stands has suggested that the greatest success in terms of increasing yield is in stands composed of species with complementary characteristics (e.g., differences in shade tolerance and height growth rates) (Kelty 2006). Other studies and reviews have also suggested

Table 5. 95th percentile regression results for aboveground live tree carbon = RD along with resulting estimates of 95th percentile and mean (ordinary least-squares regression) live aboveground carbon at current stocking levels by forest type groups.

Forest type group	b_0 intercept (Mg/ha)			b_1 RD			LAGC	
	Estimate	SE	<i>P</i> value	Estimate	SE	<i>P</i> value	Mean	95 th percentile
						(Mg/ha).....	
White/red/jack pines	−0.32	0.30	0.28	164.61	1.10	<0.01	34.89	54.32
Spruce/fir	0.23	0.24	0.34	106.33	0.99	<0.01	22.65	37.07
Southern yellow pines	1.29	0.54	0.02	161.52	1.71	<0.01	31.20	58.31
Oak/pine	−0.52	0.30	0.08	170.01	1.21	<0.01	32.72	55.47
Oak/hickory	−0.79	0.05	<0.01	192.19	0.22	<0.01	43.27	68.88
Oak/gum/cypress	−1.15	0.17	<0.01	202.56	0.79	<0.01	46.38	75.93
Elm/ash/cottonwood	−0.95	0.11	<0.01	192.18	0.78	<0.01	30.16	51.34
Maple/beech/birch	0.45	0.52	0.39	176.71	1.33	<0.01	50.96	76.29
Aspen/birch	−0.27	0.11	0.02	130.73	0.58	<0.01	23.01	36.80
Other	−0.26	0.23	0.27	155.35	1.89	<0.01	14.51	25.32
All							37.41	60.79

that complementary niche occupancy by a diverse array of tree functional groups can increase forest ecosystem productivity (Caspersen and Pacala 2001, Kirby and Potvin 2007). In the context of this study, mixtures of shade-tolerant and -intolerant species may ensure maximization of niche occupancy and hence potential maximum LAGC. Whereas shade-tolerant species can inherently tolerate a variety of stand structures and levels of stocking, shade-intolerant species flourish in a more limited set of stand conditions. Thus, forest management practices that eliminate shade-intolerant species may cause unintentional reductions in maximum LAGC. Correspondingly, the use of plantation designs or natural regeneration systems that maximize complementarity between species through spatially or temporally segregating the degree of interspecific competition may be central to achieving maximum LAGC (Kelty 2006). It is suggested that this research hypothesis be further evaluated in terms of forest product carbon life cycles and actual management treatment effects, rather than inferring management through current stand attributes. Furthermore, to apply these results in management settings, shade tolerance effects across successional stages should be ascertained within commonly managed forest types.

Although maximum LAGC was largely dependent on both tree species mixtures and stand stocking, maximum DAGC appeared to only be dependent on interspecific stocking. Woodall and Westfall (2009) found that a stand's dead wood biomass was not strongly correlated with levels of stand stocking as indicated by SDI. Trends in DAGC by interspecific stocking may suggest that increased tree species diversity results in greater niche occupancy and mortality and thus expansion of other non-LAGC stocks such as DAGC. Previous research has forwarded a "niche-complementary hypothesis," suggesting that greater functional diversity may result in greater ecosystem productivity (Srivastava and Vellend 2005, Kirby and Potvin 2007). Because dead wood may be a controlling factor of numerous ecosystem processes (Janisch and Harmon 2002, Sharik et al. 2010, Ryan et al. 2010), its positive relationship with increasing interspecific tree stocking indicates that an added benefit of mixed-species stands might include a greater potential for the detrital accretion.

Our results also highlight a substantial unrealized LAGC

stock, the difference between current levels of LAGC in understocked stands and maximized LAGC (represented by the 95th percentile of study observations). In particular, initial estimates for the entire eastern United States indicate that maximum LAGC could be more than doubled if stand conditions were altered (e.g., species selection) or stocking allowed to reach maximum levels (i.e., overstocked). Hoover and Heath (2011) also found that forest C stocks could be increased if understocked stands were fully stocked in the northeastern United States. Although stand stocking is clearly a major determinant of LAGC maximization (Hoover and Heath 2011), further research to explore management actions (e.g., species selection) that favor maximized LAGC is justified. For example, increasing the inclusion of shade-tolerant, hardwood tree species in pine monocultures of the eastern United States might facilitate increases in potential maximum LAGC. Nonetheless, altering current forest management approaches for inclusion of historically unmerchantable tree species might include tradeoffs between either maximizing sawlog production of a few tree species or the LAGC storage of a greater multitude of tree species. These tradeoffs may be inconsequential on highly productive timberland where sawlog management is the primary management objective with subsequent CO₂ sequestration in forest products, but they may provide opportunities to increase C storage on more marginal forest sites. It is suggested that future researchers explore the effects of timber product markets and resulting C storage complexities on forest stand management tradeoffs (e.g., roundwood management versus LAGC maximization).

This study is limited in its scope because it focused primarily on the maximization of LAGC with inference of management implications through extensive examination of current stand attributes across the eastern United States. An important future step is to evaluate trends in other C stocks (e.g., soil organic C and downed dead wood) by species composition and stocking. Unfortunately, these efforts are limited by very few empirical data on other forest carbon stocks relative to LAGC, resulting in most C stocks other than LAGC being modeled for national reporting efforts (Woodall et al. 2008, Heath et al. 2011). An additional limitation of this work is that it did not evaluate the flux of C from forest ecosystem stocks. A major facet of C credit trading systems is the assessment of annual C

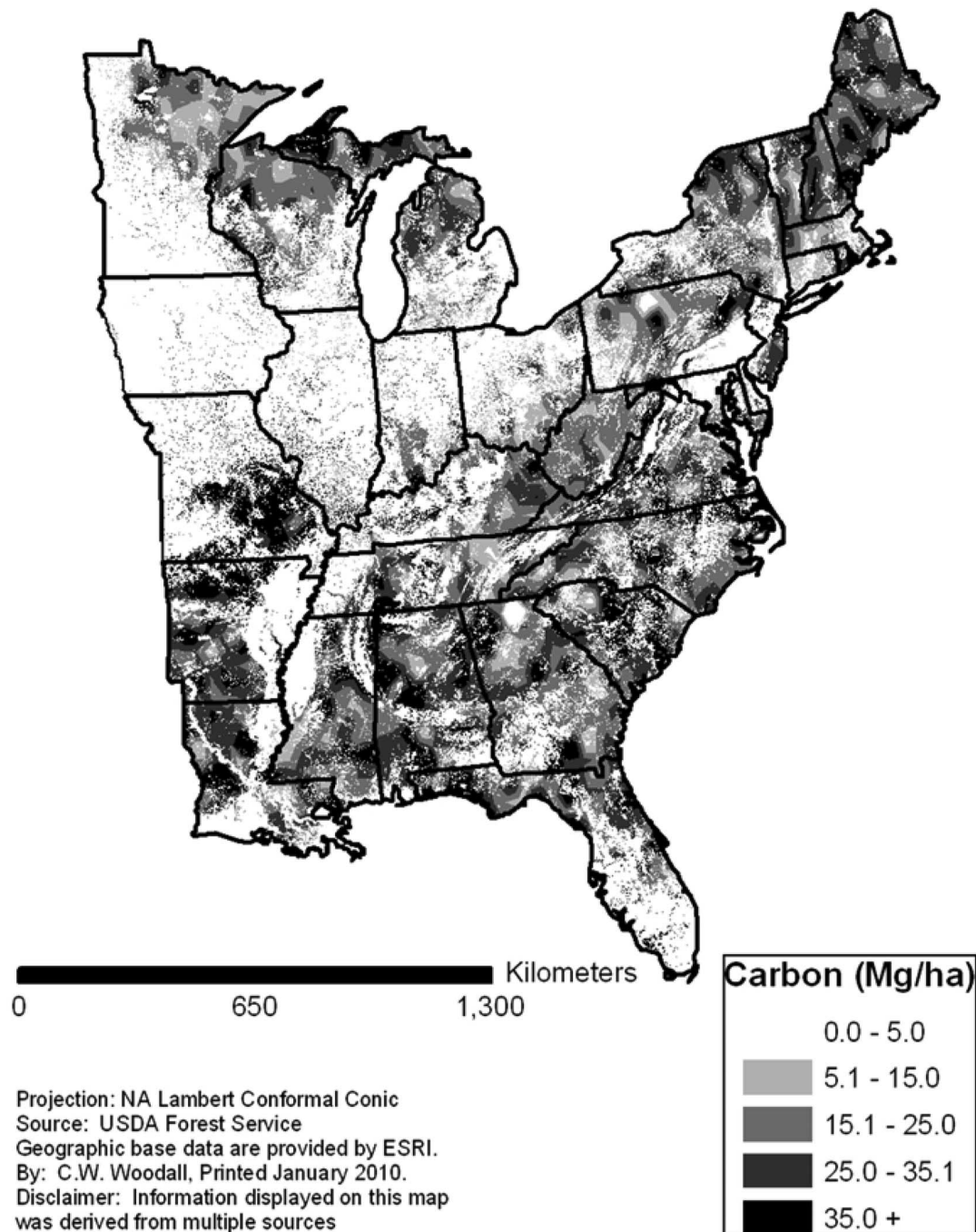


Figure 6. Inverse distance weighting of additional aboveground live tree carbon storage opportunities in forests of eastern United States.

flux (i.e., emission or sequestration). Just because LAGC can be maximized given a certain species composition and stocking level does not mean annual C sequestration will be maximized. Nonetheless, the relationships between stocking, species composition, and LAGC indicate the potential for using mixed-species stands for optimizing the performance of carbon offset projects, including the establishment of mixed-species plantations as part of afforestation projects. All inferences regarding management implications presented in this study are merely hypotheses that should be more fully evaluated through intensive research plots. Whereas extensive forest inventories may provide an unbiased estimate of current forest conditions

across a landscape, only research plots can manipulate forest vegetation to directly test management hypotheses. Finally, maximization of LAGC may come at the expense of forest health concerns such as fire hazards, individual tree resistance to pests, and loss of wildlife habitat. These tradeoffs must be considered before managing solely for maximizing LAGC.

Conclusions

As new forest management paradigms emerge for maximizing C stocks regardless of tree species or product quality, there will be increasing need to understand the dynamics

of standing tree C storage across a myriad of species and stocking scenarios. Although stand stocking is the primary driver of LAGC, this study suggests that tree species composition may greatly affect LAGC in some forests, given the same stand stocking. It is hypothesized that there may be tremendous opportunities to increase LAGC storage in eastern US forests through CO₂ sequestration-oriented forest management actions, even with stand stocking held constant. Past management of tree monocultures for maximizing growth over defined rotation lengths on productive forestland was modeled predominantly on agricultural methods. In contrast, the future of managing diverse arrays of tree species for maximizing C storage or biomass yield over undefined periods of time on marginal forestland may depend more heavily on understanding the nature of intra- and interspecific interactions and their cumulative effects on ecosystem productivity.

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